Reproductive Behavior of the Damselfish *Pomacentrus nagasakiensis* at Miyake-jima, Japan

Jack T. Moyer

Abstract The reproductive behavior of *Pomacentrus nagasakiensis* Tanaka was studied on the island of Miyake-jima, Japan, from July 1973 to October 1975. Reproductive activity began in May, when water temperatures reached 22°C and continued until early September. The heaviest concentrations of reproductive activity coincided with the waxing of the moon, reaching a peak 2~3 days prior to the full moon.

Like other pomacentrids, males construct and guard nests. Smooth sides of boulders or discarded pots, pipes, tires, etc. are used as nesting surfaces. Females are attracted with typical pomacentrid "signal jumps". Females are led to nests by an enticement display, which is clearly a distinctive action pattern from the signal jump. Spawning usually occurs in early morning or late afternoon. Several thousand eggs are laid in a single spawning. The male guards the nest and fans the eggs. Typically, a male may guard about ten patches of eggs in a season. Spawning with two or three females may occur within a few days, and a single male may care for three clutches of eggs in a single egg patch.

Males with nests in favorable locations defend their territories persistently throughout the breeding season. Territories in less favorable locations are defended only during periods of active spawning.

The following motor patterns are recognized for *P. nagasakiensis* during the courtship phase of reproduction: signal jumps, enticement, chasing, and skimming.

Introduction

Since the late 1950s, when SCUBA became an indispensable aid to marine research, the family Pomacentridae has received considerable attention as an outstanding subject for ethological research. The genus *Chromis* Cuvier has been an especially popular subject for study, with many papers appearing on various aspects of behavior (Abel, 1961; Albrecht, 1969; Fishelson, et al., 1974; Limbaugh, 1964; Myrberg, et al., 1967; Sale, 1971; Swerdloff, 1970 a, b). These studies have resulted in a growing knowledge of phylogenetic relationships within this genus.

It is rather surprising that comparatively little attention has been given to the behavior of any of the genus *Pomacentrus* Lacepède, since many species display persistent territoriality, thus lending themselves to easy observation. Low (1971) and Rasa (1969) studied teritoriality in *P. flavicauda* Whitley and *P. jenkinsi*

(Jordan and Evermann), Matsuoka (1962, 1972) reported certain aspects of the reproductive behavior of *P. coelestis* Jordan and Starks, and Honda and Imai (1973) studied breeding and development of *Pomacentrus nagasakiensis* Tanaka in the aquarium. Breder and Coates (1933) and Brinley (1939) reported on aquarium observations of spawning and egg development in two species of the closely related genus *Eupomacentrus* Bleeker.

The reproductive behavior of the damselfish, *Pomacentrus nagasakiensis* was studied near the Tanaka Memorial Biological Station (TMBS) on the offshore Japanese island of Miyake (34°5'N, 139°30'E) from July 1973 to October 1975. The results of this research are reported below.

Methods and materials

Field observations were made 3~5 times weekly in August 1973. In 1974, observations began in early May and continued 2~3 times

weekly until July 1, except for a ten day period in June. From July 1 ～ September 8, 1～3 study dives were made daily, except for August 26 and August 30, when typhoons halted observations. From September 8 ～ October 31, 2～3 dives were made per week. For the remainder of 1974, as in the winter of 1973, observations continued at 3～4 dives per month. The study continued throughout the 1975 breeding season.

SCUBA was used for all research. Various members of the TMBS staff aided in this study, totalling more than 340 hours of underwater research. Depths and temperatures were read from wrist guages. We tagged nests with plastic markers numbered with grease pencils. These were suspended from styrofoam floats and secured with lead fishing weights. Individual fish were not marked, but could usually be recognized by physical deformities, geographical location, and individual behavior, which varied considerably within the population. In 1975, plastic pipes, 18 and 25 cm in diameter, were placed in the study area as nesting surfaces. These were subsequently used in fecundity studies.

Specimens collected for taxonomic identification are preserved in the Tanaka Memorial Biological Station under the following numbers: TMBS 730726–08, TMBS 740716–02, TMBS 741120–02, TMBS 741229–01 (See Moyer and Ida, 1975).

In this paper, nests from 1973 and 1975 observations are numbered with the prefix 73 or 75, e.g. 73–01, 75–01, etc. 1974 nests are identified merely by the nest number, e.g. 1, 3, etc.

Description of study area

Observations were made at various locations around the island of Miyake; however, the major study site was in Igaya Bay on the west side of the island. The site covers an area of approximately 2500 m², ranging from 14～16 m in depth. A cliff, an ancient lava flow 2～3 m in height, is situated near the north end of the study area. North of the cliff are loose volcanic rocks and boulders resting on sand. The substrate south of the cliff consists of large chunks of broken lava, rocks, and boulders, covered with brown and red algae,

sponges, numerous soft coral, and occasional sea anemones. Further south are smooth boulders on sand. Outcroppings of table coral are scattered throughout the area.

Directly south of the cliff is a major breeding ground for *Thalassoma cupido* (Temminck and Schlegel) (Moyer, 1974). The spawning and courtship of *Stethojulis interrupta* (Bleeker), *Cirrhilabrus temminckii* Bleeker (Moyer and Shepard, 1975), *Labroides dimidiatus* (Valenciennes), and *Cheilio inermis* (Forsskål) have also been observed. Pelagic eggs of these species, especially *T. cupido*, seem to account for a considerable percentage of the diet of *P. nagasakiensis* during the reproductive season. *Chromis isharai* (Schmidt), *C. flavomaculatus* Kamohara, and *C.* sp. from breeding colonies at the cliffs nearby, and *Pomacentrus coelestis* from the boulders south of the cliffs, gather with *P. nagasakiensis* in large feeding aggregates above the spawning wrasses daily during the wrasse spawning season.

Six *Labroides dimidatus* cleaning stations are scattered throughout the study site. These are supplemented by juvenile *L. dimidiatus* at numerous places throughout the site in late summer and autumn. The abundance of cleaners may have a direct effect on the desirability of the area as a spawning site for so many pomacentrids and labrids.

Results

Pomacentrus nagasakiensis lives in loose aggregations. Our 1974 Igaya Bay study site contained an aggregation of more than 30 *P. nagasakiensis*, of which at least 18 were males. The actual nesting grounds covered an area of approximately 760 m², and included a total of 23 nests, of which no more than 18, more often 16, were defended at any one time (Fig. 1). Although the closest distance between successful nests was only 2 m, usually at least 3～4 m separated neighboring nests. Spawning commenced with the waxing of the moon in late May in 1975 and early June in 1974, continuing until late August in 1975 and early September in 1974. Differences between the years apparently resulted from the earlier full moon date in 1975. In both seasons, nesting continued with at least one nest containing eggs at all times throughout the season. Peak nesting
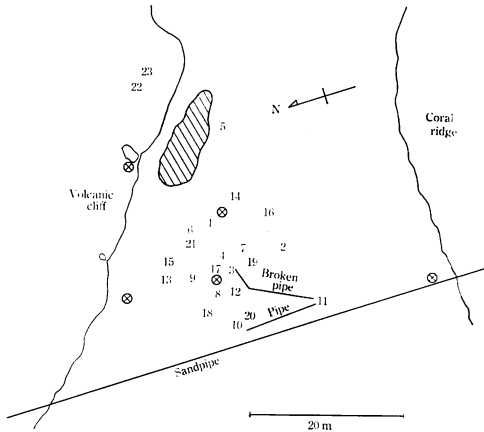
Fig. 1. Map of *Pomacentrus nagasakiensis* nesting population, 1974. Numbers show locations of nests guarded by males. The shaded area is the location of the feeding aggregate of non-territorial individuals. ⊗ = *Labroides dimidiatus* cleaning stations.

usually preceded each full moon by 2∼3 days throughout the breeding season.

Clustering behavior

The first suggestions of *P. nagasakiensis* activity begins in early May when water temperatures reach 20°C. During winter, only scattered individuals can be seen in 16∼19°C waters, and none have been observed when temperatures drop below 15°C. Reproductive behavior begins as the water temperature reaches 22°C, with "clustering behavior" (See Keenleyside, 1972). Some males move away from their nesting sites of the previous year and begin searching for new sites. Frequently, clusters of 3∼6 fish can be observed in tight groups, facing each other with deep blue foreheads. Blue foreheads normally signal appeasement in this species, and are frequently flashed by intruding males when confronted by territorial males. As none of the early season nest-hunting fish have yet established territories, this appeasement signalling is not surprising, but the meaning of tight clusters of blue-headed fish is yet to be fully understood. That it is related to the establishment of territory is suggested by the frequency and timing of our observations. In addition to numerous spring records, several similar clusters of blue-headed individuals were seen on August 20∼21, 1974, when waters warmed again after temperatures below 22°C

interrupted reproduction and territorial activities for a few days. Later, identical clusters appeared after a typhoon destroyed several nesting sites. In both of these examples, renewed nest construction, courtship, and spawning followed within a day or two.

Similar bunches of blue-headed individuals observed on one occasion in the peak of breeding activity in July, and again in late November, long after the termination of the reproductive season, confuse the picture. In both cases, these were isolated observations and may have been coincidental meetings of 3∼4 feeding fish, or, in the July sighting, males attracted to the same location away from their respective territories by a passing female. In all cases, blue foreheads would serve to inhibit aggression.

Nest construction

Frequent observations suggest that nest construction begins as soon as a suitable nesting site is found. Usually nests are on the lower surface of boulders. Construction involves removing algae and invertebrates from the nesting surface, and digging out sand, small shells, and stones. Only the male takes part in construction. Small stones and algae are carried away and dropped, and clouds of sand are blown out backwards by a rapid sculling of the caudal fin. Construction of a nest may take from several hours to more than half a day, interrupted by lengthy journeys into the water column to feed on plankton. Sometimes nests are abandoned before being used. In 1974, Nest No. 7 was abandoned and two others constructed in a period of two days. None was used.

Not infrequently, discarded junk is used as a nest site. Nest 73–04 was constructed inside a rubber tire (Fig. 2). Nest 73–12 was in an old rice pot, and nest No. 5, 1974, was in a broken piece of plastic pipe.

Courtship

a. Signal Jump

Immediately after completion of nest construction, courtship begins in the form of signal jumps ("Signalsprung", Abel, 1961) by the male. *P. nagasakiensis* is primarily a plankton feeder, and, except when guarding a nest, spends most of the day feeding in loose aggregations 3∼5 m up in the water column. These aggregations tend to center at certain locations within the

Fig. 2.　*Pamacentrus nagasakiensis* Nest No. 73–04, in a discarded tire.

borders of the breeding ground. When visibility is good, it is possible to see the entire breeding ground from 5 m above the substrate. Therefore, signal jumps from nearby nest sites are easily visible from feeding positions in the water column. Signal jumps begin as the fish swims slowly straight upward, propelled only by simultaneous stokes of the pectoral fins, to a point perhaps 4 m above the substrate. The caudal fin remains motionless. Suddenly, he darts downward, usually in the direction of his nest, with 3∼4 fast sculling motions of the caudal fin. The downward dash takes him about 1 1/2∼2 m below the apex of the display. He then drifts up and repeats the pattern. Most frequently, signal jumps are performed in the immediate vicinity of the nest, but occasionally the nesting male may go quite some distance to attract a female with the looping display. The male from nest No. 14 was observed signal jumping 20 m from his nest, near the feeding aggregation.

Signal jumps are often performed at random, with no specific female in the immediate vicinity. At such times, the signalling fish remains in the normal color phase. However, if a female moves into visual range, the signalling action pattern increases in speed, and the enticement color

phase begins to appear. Enticement colors remain faint during signal jumps, but become vivid and obvious when actual enticement begins. An excellent photograph of *P. nagasakiensis* in the enticement color phase was published by Honda and Imai (1973).

b.　Enticement

Enticement is an entirely different action pattern from the signal jump, although enticement colors sometimes begin to appear in the signalling phase, and thus may be transitional between the two action patterns. During enticement, three blotchy grey bands appear on the body; one extending from the top of the head over the eye to a point directly behind the eye, another from about the third dorsal spine to the lateral line or slightly lower, and the third directly anterior to the caudal peduncle. These vary from dark grey in signal jumps to almost white in intense enticements.

The enticement display begins with the male rushing toward the approaching female in the blotchy color phase, quivering and swimming with exaggerated motions of the caudal and pectoral fins. As he approaches a point 10∼15 cm from her, he abruptly turns and dashes back toward his nest, returning again and again, always in the same rapid exaggerated,

quivering swimming motion and blotchy color. In this way he attempts to lead the female to his nest. Enticement motions are always oriented on a direct line between the female and the nest. The rapid caudal and pectoral beat continue throughout, while both approaching and leaving the female.

Enticement only rarely results in spawning. Not infrequently the female follows the enticing male to his nest, but she rarely spawns. On one occasion, a female was followed for more than 15 min. She ranged freely over almost the entire breeding colony. She entered five nests, attracted by enticement displays, but did not spawn. Males enticed her out of other male's nest sites, but no agonistic postures nor chases were observed. Males moved far from their nests (8~10 m) to entice the female. They showed a variety of intensities of the blotchy enticement color phase. Some turned it off as soon as she entered their nests, returning to their normal color phase, but others, e.g. No. 13, remained blotchy throughout. It is not uncommon to see 4~5 males enticing a female at the same time, while another, a few meters away, performs signal jumps in faint enticement colors.

Pomacentrids are known to produce sounds in courtship (Allen, 1972; Verway, 1930). On numerous occasions, *P. nagasakiensis* males were heard producing grunting sounds while enticing females.

Rarely, the male on territory may show some agonism toward an invading male. On one occasion (July 23, 1974), No. 10 was enticing a female when No. 8 interrupted and attempted to attract the female toward his nest. No. 10 touched him on the side with his mouth and extended all of his fins, but did not chase or bite. Eventually No. 8 enticed the female away from his rival. Actual aggressive chasing of a male by another male was observed only rarely. For example, No. 12 attempted to entice a female away from No. 8, and was aggressively chased. Normally, little, if any agonism seems to be displayed between males during mutual courtship of a female.

c. Chasing

Typically, signal jumps begin courtship displays. As soon as a female comes into sight, most males in the vicinity attempt to attract her
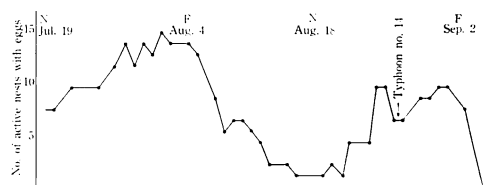

Fig. 3. Nesting success of *Pomacentrus naga-sakiensis* in relation to stages of the mean in July, August, and early September, 1974. N=new moon, F=full moon.

attention in this manner. As she approaches, the signal jumps cease, and enticement displays begin. If these fail and the female moves on, aggressive chasing and, rarely, biting follow. In the rare cases when such attacks attract the interest of the female, enticement begins again. Chasing of this nature is usually, but not always, performed by males in the enticement color phase.

Chasing of females by males as a stage of courtship is normally an action that follows unsuccessful attempts to entice the female into the nest. There are exceptions. No. 8 not infrequently left the signal jump phase to aggressively chase and sometimes bite the approaching female. Interestingly, No. 8 was by far the most successful nesting male in 1974 (Fig. 4).

d. Spawning

Spawning commences with the male leading the female into the nest with the enticement display. The female touches the surface of the nesting rock with her lips, turns over and begins rubbing her abdomen over the surface of the rock with rapid beats of her pectoral fins and a shuddering of the body. Her ovipositor protrudes about 2 mm. Creamy eggs are deposited densely in a gradually widening patch over the rock surface. The male follows behind, no longer in blotchy enticement colors, occasionally touching the eggs with his lips, then turning over, his abdomen and protruding genital papilla appearing to rub over the freshly deposited eggs. This is the "skimming" of Myrberg, et al., 1967. His body quivers constantly as he propels himself with his pectoral fins in circles over the eggs. Not infrequently, either or both fish may leave the nest for 2~3 sec, immediately withdrawing their genital papillae. Sometimes the male leaves the nest to go into quivering enticement
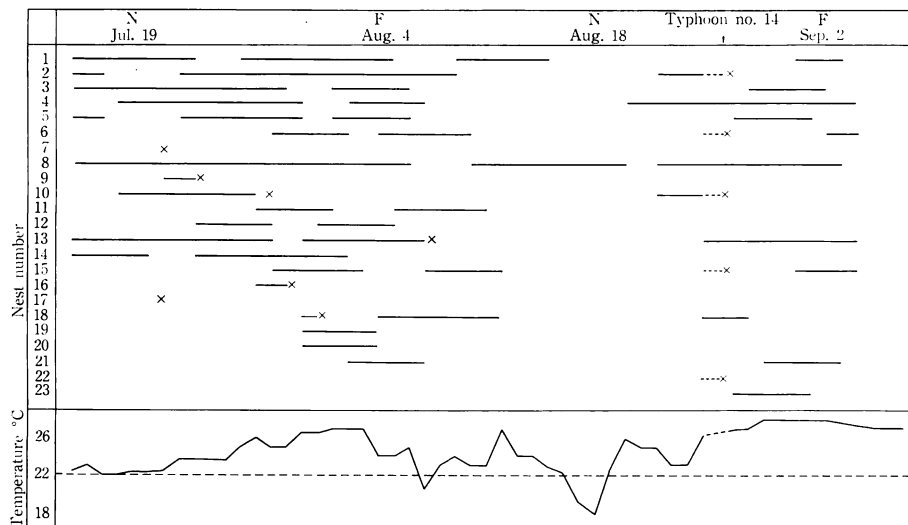
Fig. 4. Graph showing nesting success of individual *Pomacentrus nagasakiensis* males, Jul. 15–Sep. 7, 1974. Bars indicate periods when nest contained eggs. Dotted bars indicates no observation possible due to typhoon seas. ×=nest destroyed or abandoned. The dotted line at 22°C indicates the apparent minimum temperature of reproductive activity. N=new moon, F=full moon.

display with blotchy colors, returning seconds later in normal colors to deposit more sperm, after first touching the eggs with his lips. Both male and female occasionally stop spawning to fan the eggs.

At the conclusion of spawning, the female leaves the nest, with the male often attempting to lead her back with a rapid enticement display. After a moment, he may touch her abdomen with his lips, seem to lose interest and return to the nest to fan the eggs.

Eggs are laid in densely compact clusters, our samples varying from 160×95 mm to 230×190 mm in size. Eggs are oblong in shape, 0.5 mm×1.25 mm. They are creamy in color when first deposited, changing to white, grey, and finally silvery-grey before hatching.

Males continue to entice females, even after eggs are in the nest, and spawning usually occurs while eggs are already being tended. Nest No. 8 often contained three separate clutches of eggs simultaneously. Usually the No. 8 male was able to entice another female into his nest to spawn almost as soon as hatching eggs made space available, and therefore, he almost continually tended eggs (Fig. 4). Similar polygamous behavior occurs in *P. coelestis* (personal observation).

Spawning and courtship were most frequently observed before 8:30 AM and after 3:00 PM. Mid-morning reproductive activity was regular, but infrequent, apparently limited by almost daily morning feeding on the gametes of spawning *Thalassoma cupido* in the center of the *P. nagasakiensis* colony.

Care of eggs

Only the male tends the nest. Females move from male to male, with no attachment to any nesting territory, and males continue to entice passing females while tending eggs.

Males with eggs rarely leave the vicinity of the nest, although short trips away from the eggs are rather common. These journeys vary from a few seconds to 6~8 min, and are usually to the water column nearby to feed on plankton or wrasse eggs, or to a *Labroides dimidiatus* cleaning station. Activity at the nest consists of cleaning out debris and fanning the eggs. Occasionally, the male touches the eggs with his lips. This action is apparently analogous to the "mouthing" of eggs in *Amphiprion*, described by Allen (1972) and others. In such cases, dead eggs are removed.

Fanning postures have been described by Honda and Imai (1973) and will not be repeated

here.

Nests are guarded from potential enemies. Most frequently the pursued fish is *Thalassoma cupido*. In addition, the following species have been observed being chased or attacked: *Thalassoma lutescens* (Lay and Bennett), *Pteragogus flagellifera* (Valenciennes), *Coris* sp., *Halichoeres prosopeion* (Bleeker), *Choerodon azurio* (Jordan and Snyder), *Stethojulis interrupta*, *Chromis isharai*, *Pomacentrus coelestis*, *Plotosus anguillaris* (Lacepède), *Pseudupeneus spilurus* (Bleeker), *Chaetodon nippon* Steindachner and Döderlein, *Synodus variegata* (Lacepède), and *Gymnothorax kidako* (Temminck and Schlegel).

We have witnessed attacks on crabs, *Percnon planissimus* (Herbst) and shrimp, *Palaemon pacificus* (Stimpson), in successful attempts to drive them from the nest.

We were sometimes attacked while examining eggs. Usually the defender rushed directly at us to a point a few centimeters from our masks, suddenly turning at right angles and stopping, with all fins extended. Some fish were more aggressive than others. Nos. 73–01, 73–03, and No. 2 (1974) usually defended by backing into the hand of the observer, with thrashing caudal fins. Nos. 73–02, and 5, 8, and 18 (1974) always made frontal attacks, biting the observers hand or arm. Frequently clicking noises were heard just before the attack. Both Nos. 5 and 8 attacked their nest tags, and No. 8 actually managed to carry his tag, with its comparatively heavy lead weight, 5 m from the nest.

Despite aggressive defense of eggs and nests, many clutches of eggs are destroyed by predators. We were never able to identify the responsible fish or invertebrate, although *T. cupido* was once seen eating cases of hatched eggs. Nest No. 16 was destroyed, the eggs eaten, and the male apparently killed. Two morays, *Gymnothorax kidako*, lay in the nest hole, and two shrimp, *Palaemon pacificus*, were on the rock surface where the eggs had been. The defender was never seen again. Shrimp usually move into empty nests, apparently to eat the egg cases, and may account for destruction of eggs from time to time.

Eggs hatch on the fourth or fifth night after spawning, varying apparently with water temperatures.

Fecundity and male nesting success

Pomacentrus nagasakiensis is a multiple spawner. Spawning occurs at any time between June and September, reaching peaks as the moon waxes. Eggs are small, egg patches are large, and the incubation period is short. Therefore, one would expect the fecundity of this species to be rather high among pomacentrids. Since we did not examine ovaries, we can only approximate fecundity of females on the basis of male nesting success.

Pieces of plastic pipe, 25 cm in diameter and 24 cm in length, were placed in the midst of the breeding grounds. Eggs laid in these pipes were counted in the laboratory using a dissecting microscope. Having thus determined the number of eggs per cm^2, it was possible to make estimates of the number of eggs in a particular egg patch. The average nest patch computed in this way contained about 21,000 eggs.

Since observations were made almost daily, it was possible to rather accurately estimate the number of egg patches guarded by each male during the breeding season. There was considerable variation in nesting success between males. In 1974, No. 8 had eggs almost all the time, and since there was much overlapping of clutches, it was rather difficult to reach our estimate of 14 nest patches and about 294,000 eggs for his nest. Nos. 6, 11, 12, and 14 were least successful of those fish regularly performing signal jumps and enticements, with about five egg patches and 105,000 eggs for the year. Nos. 1, 2, 3, 4, 5, 10, and 13 had nests with eggs about 10 times, amounting to approximately 210,000 eggs each. From this we can estimate the average number of eggs tended by a single male to be somewhere between 200,000~220,000 eggs in a season. Based on their studies of *P. nagasakiensis* in Kyushu, Honda and Imai (1973) estimate fecundity of this species at 211,000 eggs.

Discussion

a. Lunar periodicity and spawning

The influence of the moon on the reproductive behavior of marine animals is well known (Korringa, 1947). Among the pomacentrids, Allen (1972) has shown lunar periodicity for spawning of various species of *Amphiprion* at Eniwetok. That the spawning of *P. nagasakiensis* is influenc-

ed by the moon is clearly shown in Fig. 3. As the moon waxes, spawning increases. At the July, 1974, new moon, only 6 nests had eggs. This number increased to 10 by the first quarter and reached a peak of 14 three days before the full moon. After the full moon, there was a sudden decrease to a minimum of one nest with eggs two days before the new moon. In August, nesting activity began to increase shortly after the new moon, reaching 9 nests with eggs by the first quarter. Typhoon No. 14 destroyed five nests shortly after, but new eggs in other nests brought the total up to 9 again two days before the full moon.

In both months, peak activity preceded the full moon by 2~3 days. Allen (1972) suggests that increased nesting as the full moon approaches might improve conditions for nocturnal egg care. Albrecht (1969) found increased egg care at night in two species of *Chromis*, adding weight to Allen's point. Larvae of *Amphiprion* and presumably other pomacentrids are positively phototactic, and, as Allen suggests, a bright moon might stimulate freshly hatched larvae to rise and join the plankton. Since peak nesting comes 2~3 days before the full moon in *P. nagasakiensis*, and since incubation is only 3 1/2~4 1/2 days, most eggs hatch within a few days of the full moon, providing maximum light conditions for the hatchlings. However, much moonlight remains in the third quarter. Therefore, if phototaxis is a factor, preference of *P. nagasakiensis* for the waxing moon suggests an early evening hatching hour. This possibility is supported by the fact that Honda and Imai (1973) found hatching to occur within an hour after sunset, and that the larvae were attracted to aquarium lights.

Cold water had a negative influence on spawning during the third quarter in August, when the water temperature plunged to 18.5°C and stayed below 20°C for two days. During this period, many nests were abandoned, and no signal jumps nor enticements were observed. The temperature reached 22°C by the new moon, and nest construction and spawning began shortly after. A remarkable drop in nesting activity had been noticed prior to the temperature decrease. The sudden drop in reproductive activity after the September full moon was clearly not related to water temperature, which

remained at 26~28°C for the next month.

b. Clustering behavior

Clustering behavior was first observed by Clarke (1971) among the garibaldi, *Hypsypops rubicunda* (Girard). He suggested that such behavior might represent a form of communal courtship beginning prior to the regular breeding season. Keenleyside (1972) described similar behavior in *Abudefduf zonatus* (Cuvier), and was the first to use the term "clustering behavior". He suggested that clustering might contribute to breeding synchrony in local populations. Moyer and Sawyers (1973) observed clustering in colonial nesting *Amphiprion clarkii*, again relating it to courtship behavior. Sale (personal communication) has observed such behavior in various Australian pomacentrids and identifies it with the term "visiting behavior". In *P. nagasakiensis*, clustering occurs most frequently just prior to periods of intensive nesting, fitting well with the findings of Clarke (1971) and Keenleyside (1972). Clustering appears to be a widespread behavior pattern in pomacentrids, and further studies of its various forms and functions are needed.

c. Territoriality

Studies of pomacentrid fishes have shown that many are territorial only during periods of reproductive activity, e. g. *Chromis chromis* (Abel, 1961), *C. multilineata* (Myrberg, et al., 1967), *C. ovalis* (Steindachner) and *C. verator* Jordan and Mets (Swerdloff, 1970 a), *C. isharai* and *C. albomaculata* Kamohara (personal observation), *Dascyllus albisella* Gill (Stevenson, 1963), *Abudefduf abdominalis* (Quoy and Gaimard) (Helfrich, 1958), and *A. saxatilis* (Linnaeus) (Fishelson, et al., 1974). Others, such as various species of *Amphiprion* (Allen, 1972; Moyer and Sawyers, 1973), *Hypsypops rubicunda* (Limbaugh, 1964; Clarke, 1970 and 1971), *Abudefduf lacrymatus* (Quoy and Gaimard) and *A. leucozona* (Bleeker) (Fishelson, et at., 1974) persistently defend territories.

Both types of territoriality are found in the genus *Pomacentrus*. Fishelson, et al. (1974) found *P. albicaudatus* and *P. trichourus* Günther holding permanent territories, and Rasa (1969) reports the same for *P. jenkinsi*. Low (1971) reported *P. flavicauda* Whitley defending the same territory over a period of five months, and Bardach (1958) suggested permanent territoriality

for *P. fuscus* (Cuvier) and *P. leucosticus*. On the other hand, our studies of *P. coelestis* at Miyake show it defending territory only during periods of active nesting.

Pomacentrus nagasakiensis seems to demonstrate yet a third type of territoriality. Some individuals hold permanent territories and defend them throughout the breeding season. Others return to their nest sites and become territorial only during periods of spawning, and a third type changes the location of his nest site and territory one or more times during the reproductive season.

Allen (1972) points out that those species that defend territory only during reproductive activity are primarily plankton feeders and, therefore, do not need to permanently defend a limited area in order to protect their food supply. This explanation suffices for *P. coelestis*, a plankton feeder, but not for *P. nagasakiensis*. Although the latter almost exclusively feeds on plankton, many individuals are territorial throughout the breeding season. Furthermore, those holding permanent territories seem to have the highest reproductive success. For example, in 1974, males Nos. 1, 3, 4, 5, 8, and 13 held permanent territories and tended the most clutches of eggs. Nos. 2, 10, 11, and 12 returned to their territories only to spawn and had somewhat less successful reproductive records. Nomadic individuals, such as the male that occupied both nest Nos. 9 and 21 and that at Nos. 7 and 19. were the least successful of all (Fig. 4). An exception is No. 6, who defended his nest site from June to September but had a very poor spawning record.

Apparently, once a favorable nesting site is secured, it must be guarded continuously or risk loss to another male. Males defending sites that for some reason may not be "suitable" defend them only at spawning peaks, spending most of their non-spawning time feeding on plankton, often far from their nests. Just before spawning, they alternate between repairing their previous nesting site and looking for a new site. Territoriality, then, appears to be directly related to the "desirability" of the nesting site, with the most suitable locations defended constantly.

Two obvious factors contribute to a suitable nest site. One is the presence of a relatively smooth surface of sufficient size to permit spawn-

ing to take place. Secondly, the substrate must be solid in order to provide absolute or near-absolute protection from the rear. Pipes, rice pots, tires, etc., are ideal for this purpose, if large enough. In fact, if available, they are invariably defended throughout the spawning season, even if somewhat isolated from the rest of the aggregate, e. g. No. 73–04. Brinley (1939) recorded a similar use of discarded junk in the form of cans, bottles, and even an old shovel, as nesting sites of *Eupomacentrus leucosticus* Müller and Troschel, and Matsuoka (1962) was able to get *Pomacentrus coelestis* to spawn in pieces of pipe placed in the study site for that purpose. As for a natural nest site, boulders on a sand substrate seem to be favored, since nests can be constructed with comparative ease by fanning out the sand.

Nests that seemed least desirable, e. g. 7, 9, 19, and 21, were located at relatively small boulders that were either too upright to provide the limited shelter apparently required, or were too small and cramped to permit ideal spawning.

A third factor seems to be related to shelter from surge during storms. This is especially true where the substrate is sand. 1974 nests Nos. 2, 7, 10, 11, 19, and 20 were all in a long, shallow depression, where surge was strong. None was defended persistently. All were destroyed by drifting sand during Typhoon No. 14, and the male from No. 2, easily identified by his split caudal fin, was never seen again. Robins (1957) noted that sand abrasion of the gill filaments and physical exhaustion are common causes of death during storms.

Obviously, the availability of females is an important factor in the establishment of a permanent territory. A major mixed concentration of feeding pomacentrids, including most of the female *P. nagasakiensis* in the population under study, was observed almost daily in each year near the top of the cliff, close to Nest No. 5. A weak current flowing seaward causes upwelling along the cliff at that point, presumably resulting in concentrations of plankton in the comparatively narrow water column above the cliff. Signal jumps were performed in the vicinity of this group by Nos. 1, 5, 6, and 14. Once attracted to any of these males, signal jumps from the cluster of nests including Nos. 3, 4, 7, and 19, could and often did lure females in their direc-

tion, where the signalling of other males became noticeable.

Labroides dimidiatus cleaning stations may also contribute in some way to the establishment of permanent territories. The successful cluster of nests 3, 4, 8, 12, and 18 were all within a few meters of a cleaning station, as were Nos. 1 and 14. Individuals from these nests were often seen taking short trips to the wrasses. Cleaner wrasses also bring females within enticement range of males nesting relatively far from the feeding aggregate.

The possibility that cleaning stations may contribute to the nesting success of this species adds a new dimension to the studies of Slobodkin and Fishelson (1974), which suggest that pomacentrids are relatively unaffected by the presence of *Labroides dimidiatus*.

Since competition for food is not a factor in the territoriality of *P. nagasakiensis*, due to its preference for plankton, active competition for nest sites seems to be the most important purpose for the establishment of territories. Competition for control over the most suitable sites is severe, demanding persistent defense of such territories once secured. In the population under study, sexually active males apparently outnumbered ideal nesting sites, resulting in the different types of territoriality described.

d. Fecundity

Fecundity varies widely within the pomacentrids. Turner and Ebert (1962) estimated 615,000 eggs for *Chromis punctipinnis* (Cooper) and Garnaud (1957) put *Dascyllus trimaculatus* (Rüppell) fecundity at 340,000~425,000 eggs. Clarke (1970) found the average for *Hypsypops rubicunda* to be 129,000 eggs. At the other extreme, Allen (1972) estimated 3,000~5,000 eggs per year for *Amphiprion chrysopterus* Cuvier and 2,000~4,000 eggs for *A. perideraion* Bleeker. Therefore, our estimate of *Pomacentrus nagasakiensis* males guarding 200,000~220,000 eggs is about average fecundity among pomacentrids so far studied.

Possible reasons for differences in fecundity are discussed by Swerdloff (1970). Highest fecundity is found among fish with pelagic eggs. Nest-guarding pomacentrids have a much lower fecundity, as would be expected. Variation within the pomacentrids may be due to such factors as vulnerability of eggs, i. e. nest location

(Stevenson, 1963). Species with concealed nests or those protected by sea anemones would have the lowest fecundity. *Pomacentrus nagasakiensis* eggs contrast with the dark rocks on which they are deposited, and little effort is made to conceal the nests. Therefore, eggs are rather vulnerable to predation. Futhermore, like *Dascyllus* and *Chromis*, *Pomacentrus* eggs hatch early. This means that the larval fish are smaller, less efficient swimmers, and more subject to predation than the more developed *Amphiprion* species that hatch in relatively advanced stages after 6 1/2~12 1/2 days (Allen, 1972; Bell, in preparation).

e. Sequential behavior patterns in reproduction

Much attention has been given to analysis of behavior patterns and their usefulness in tracing phylogenetic relationships in pomacentrids (Reese, 1964; Myrberg, et al., 1967; Sale, 1971; Swerdloff, 1970 a). Swerdloff (1970 a) proposed the following sequence of reproductive behavioral phases: territorial delineation, preparation of nest site, courtship, spawning and fertilization, and parental care of eggs. Reese (1964) added "selection of nest site" as a separate phase. In *P. nagasakiensis*, selection of nest site and territorial delineation seem to be too closely related to be distinguished as separate phases.

Within the courtship phase, the most well-known of motor patterns in pomacentrids is the signal jump, first described by Abel (1961). Swerdloff (1970 b) divides courtship into two parts: the signal jump and skimming (see Myrberg, et al., 1967). Albrecht (1969) added "chasing", which he considered closely related to signal jumps, and Sale (1971) described a "high intensity signal jump". None of these authors described enticement as a distinctive action pattern, although Sale's "high intensity signal jumps" have some similarities.

In *Pomacentrus nagasakiensis*, enticement can be clearly recognized as a distinct behavioral pattern, easily distinguishable from signal jumps that usually precede it, and subsequent chasing and spawning that may or may not follow. Certain aspects of enticement may be transitional with signal jumps and spawning, e. g. the blotchy enticement color phase. However, the enticement action as a whole is distinct. An almost identical enticement pattern occurs in *P. coelestis*, including blotchy enticement colors

Fig. 5. A typical nest of *Pomacentrus nagasakiensis*, showing white egg patch. (Nest No. 1, 1974)

(personal observation). We have observed similar enticements in *Abudefduf sexfasciatus* (Lacepède) in the Bonin Islands, *Chromis flavomaculatus*, *C.* sp., and *Pomacentrus marginatus* Jenkins. Fishelson, et al. (1974) describe pomacentrids "leading the females to spawn" after "signal swimming", but they do not elaborate. We propose the following sequence of courtship behavior patterns for comparative studies of pomacentrid fishes: signal jumps, enticement, chasing, and skimming.

Not all of these patterns occur in all pomacentrids. For example, we have never observed signal jumps in *Pomacentrus coelestis*, presumably due to its small size and vulnerability to predation if such an action pattern occured. Similarly, Russell (1971) found no signal jumps in *Chromis dispilus* Günther. The limited home range of various species of *Amphiprion* eliminate their need for signal jumps and enticements. The lack of any of the proposed pre-spawning behavioral patterns in a particular pomacentrid can probably be explained with study. Such explanations would contribute to a better understanding of the evolutionary development of the family.

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(Tatsuo Tanaka Memorial Biological Station, Toga Farm, Ako, Miyake-jima, Tokyo 100–12 Japan)

ナガサキスズメダイの産卵生態

Jack T. Moyer

三宅島において 1973 年から 1975 年にかけナガサキスズメダイの産卵生態を潜水観察により調査した. 産卵行動は水温が 22℃ に達する 5 月に始まり 9 月上旬まで続き, その頻度は月齢と関連があり満月の 2, 3 日前に最も活発となる. 他のスズメダイ類と同様に雄が転石, タイヤ, パイプ等の面を掃除し産卵床を造り卵塊を保護する. 産卵は通常早朝あるいは夕方に行なわれるが求愛―産卵の際の雄の一連の行動は①signal, ②enticement, ③chasing, ④skimming の 4 形に分けられそれらは泳ぎ方, 方向性, 体色等で明瞭に区別される. 雌は 1 回の産卵で数千の卵を産み, 雄は通常 1 産卵床の中に 3 つの発生段階の異なる卵塊を保護し, 受精卵は 5 日目の夜に孵化し 1 繁殖期にほぼこの過程を雄は 10 回繰り返す. 縄張り性は産卵期間のみに発達し, その強さは産卵床の好適性と関連しており, 好適な場所ほど強固にかつ長期間守られ孵化する個体数も多い.

(100–12 東京都三宅島阿古 富賀農園 田中達男記念生物実験所)